Vision Research 48 (2008) 2269–2274

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Long-wave sensitivity in the masked greenling (*Hexagrammos octogrammus*), a shallow-water marine fish

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ARTICLE INFO

Article history:
Received 11 March 2008
Received in revised form 5 June 2008

Keywords:
Fish vision
Visual pigments
Cones
Ocular media

ABSTRACT

Microspectrophotometry (MSP) revealed that surprisingly for a "fully marine" species, in summer, photoreceptors of the nearshore scorpaeniform fish known as the masked greenling, *Hexagrammos octogrammus*, contained exclusively, or presumably, porphyropsin with a small admixture of rhodopsin. As a result of this, the λ_{max} of the spectral sensitivity of the photoreceptors were significantly shifted to longer wavelengths as compared to the λ_{max} typical of marine shallow-water fishes, showing about 530 nm for rods and single cones, and 570/625 nm for double-cone members. These unique spectral shifts would permit a cone-driven wavelength discrimination in spite of high-density orange corneal filters which block light at lower wavelengths.

1. Introduction

The masked greenling *Hexagrammos octogrammus* was the first species of fish for which a new unique phenomenon in visual optics was found, namely changeable colouration of the eye cornea (Orlov & Gamburtzeva, 1976). It appears as the dependence of the optical density of the cornea on the ambient illumination. The cornea is heavily pigmented when exposed to bright light, but becomes colourless in the dark. It has been demonstrated that the full recolouring of the cornea occurs by the movement of orange and yellow carotenoid pigments in the specialized chromatophores with long processes shading the pupil zone. These changes can take about 1 or 2 h depending on the ambient illumination and temperature (Appleby & Muntz, 1979; Kondrashev & Gnyubkin, 1999). It is pertinent to note that such unusual corneal chromatophores were probably first described observations of the mottled sculpin (*Cottus bairdi)* but without mentioning its sophisticated light-shading mechanism (Walls & Judd, 1933). The authors compared the pattern of the "very long heavily pigmented" cell processes as having an effect of "yellow waterfall".

For over 30 years since the discovery of fish with changeable corneal pigmentation, the list of fish species with this particular feature has grown (Heinermann, 1984; Kondrashev, Gamburtzeva, Gnjubkina, Orlov, & Pham Thi, 1986; Siebeck, Collin, Ghoddusi, & Marshall, 2003; Siebeck & Marshall, 2001; see also at http://cool.-iitp.ru/projects/posters/cornea/). However, the masked greenling remains the only species whose cornea has most intensive colouration in the day time. The pigment density in the pupillary zone is extraordinarily high and can reach 4 log units at longer wavelengths (Orlov & Gamburtzeva, 1976). Such spectral and light intensity changes introduced by the alterations of the corneal colouration can dramatically affect visual discrimination. Generally, the fish photoreceptor system corresponds well to the spectral properties of the environment (Loew & Lythgoe, 1978; Lythgoe, 1972), and the existence of such a densely coloured optic filter raises the question of how the fish overcomes the evident losses of the overall visual sensitivity and colour discrimination, and whether there is a match between the spectral properties of the photoreceptors and the cornea. The present paper is aimed at the study of the spectral sensitivity of retinal photoreceptors in the masked greenling using microspectrophotometry (MSP).

2. Materials and methods

2.1. Material and preparation

The masked greenling *H. octogrammus* (Pallas, 1814) inhabits temperate coastal waters of the North Western and Northern Pacific at shallow depths. The species follows the diurnal benthic mode of life and has never been found in the waters of lowered salinity (Gomelyuk, 2000; Gomelyuk, Gamburtzeva, & Sakharov, 1989; Novikov, Sokolovskii, Sokolovskaya, & Yakovlev, 2002; Rutenberg, 1970). The fish, mostly adult individuals of both sexes 15–20 cm in length were caught in May–October with cage nets and a beach seine in Vostok Bay (Peter the Great Bay, Sea of Japan) at a depth of 1–10 m. The fish were treated in accordance with the ECC Directive of 24 November 1986, and experimental procedures were approved by the Scientific Council of the Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences (IMB FEB

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doi:10.1016/j.visres.2008.07.004

RAS). Prior to experiments the specimens were housed for two to seven days in the indoor aquaria of the Vostok Biological Station (IMB FEB RAS) at 10–17 °C under a natural light cycle. Before the experiment the fish were dark adapted for 3–5 h, euthanized with an overdose of MS222 and decapitated. The eyes were enucleated and the cornea, lens, and vitreous humour were removed. The retina was separated from the pigment epithelium, and a small piece from the central or a peripheral part was prepared for MSP. All procedures were performed under IR illumination using a CCD camera (WATEC Co.) and low-power stereomicroscope. The image was displayed on a b/w monitor covered with a deep-red plexiglas filter.

To determine the nature of the chromophore group of pigments, we used the well-known reaction of oxidation of rhodopsin and porphyropsin in the presence of hydroxylamine with the formation of light-stable products (oximes), whose spectral characteristics could be easily measured. According to the estimation by difference spectra the wavelength of maximum absorbance of A_1-oxime absorption lies at 367–368 nm, and that of A_2-oxime—at 386–387 nm (Bridges, 1972). Thus, the right shoulders of the oximes' absorption curves are 20–30 nm apart at a given wavelength and are reliably distinguishable. Hydroxylamine sulphate (FLUKA) was dissolved in normal saline (0.9% NaCl) to 20–40 mM and adjusted to pH 7.2 using 3 M NaOH solution. The retina isolated from the eye globe in the dark was then kept in hydroxylamine solution for 10–15 min. It was then completely bleached under a table lamp or by an exposure to the daylight. Then photoreceptors were isolated and measured by MSP as described below.

2.2. Microspectrophotometry

Spectral absorbance of the outer segments of retinal photoreceptors was measured according to the accepted protocol described in detail elsewhere (Bowmaker et al., 1994; Collins & MacNichol, 1984; Govardovskii, Fyhrquist, Reuter, Kuzmin, & Donner, 2000; Sillman, Spanfelner, & Loew, 1990; White, Goncalves, Partridge, & Oliveira, 2004). MSP was carried out using a single-beam device with a "jumping stage" (Govardovskii & Zueva, 1988), the spectra were recorded under computer control with an AD converter. This was the same basic instrument with a dry quartz-mirror condenser (40×, NA 0.5) and a 40×, NA 0.95 microscope objective (both from LOMC, Russia) that were used earlier for measurements on Baikalian fishes (Bowmaker et al., 1994). To avoid bleaching, only a single scan was used over the range of 360–750 nm at 1-nm intervals and a scanning speed of about 20 nm/s. Records were made on isolated cones or on groups ("bunches") of the outer segments of thin rods.

2.3. Corneal transmission

The corneal transmission was measured using a Perkin–Elmer 555 (Sweden) spectrophotometer. The non-fixed cornea isolated from the eye was placed between two cover glasses and exposed to the measuring beam. The measurement area in the central part of the cornea was limited with the help of a circular diaphragm (2 mm in diameter). The zero-line of the instrument was adjusted beforehand with the use of an equivalent diaphragm placed in the reference beam.

2.4. Data processing

For a preliminary evaluation of spectral maxima, the absorbance values where fitted with templates for vitamin A_1- and A_2-based visual pigments proposed by Govardovskii et al. (2000) and the curve fitting software (TABLECURVE 2D, SYSTAT Software Inc.). The raw data for each record, without smoothing, were normalized, and the best fit was found for the long-wave limb between 30% and 70% of the maximum. The same program showed λ_{max} as an argument value, when the 1st derivative of the resulted template curve equaled zero. Since the spectral characteristics of the visual pigments of the masked greenling were not previously reported, the above procedure could not yield their actual characteristics. However, this approach allowed us to determine the boundaries of the spectral classes of photoreceptors of every type. Herewith, the difference between the results of approximation by nomogram curves for A_1- and A_2-pigments did not exceed 7 nm. A preliminary estimation was important for further processing of the experimental data which included summation and averaging of raw recordings from many cells, zero-line correction, template fitting, and, in some cases, digital filtering for noise reduction according to the procedures described earlier (Govardovskii et al., 2000).

3. Results

3.1. Corneal colouration

Changes in the cornea colour of the masked greenling are due to reversible pigment movement within the multilayer framework of highly specialized chromatophores. The bodies of these cells are located at dorsal and ventral corneal margins (Fig. 1A–C) and a single long process protrudes to the central (pupil) zone (Fig. 1D). The optical density is very high in bright daylight (more than 3 log units), with the index T50 (the wavelength at which 50% of the maximal transmittance is reached (Douglas & McGuigan, 1989)) being as high as 575 nm (Fig. 1E). This "cut-off"-filter does not practically transmit light with a wavelength shorter than 520 nm.

3.2. Visual pigments

The retina of the masked greenling *H. octogrammus* has a structure typical of the majority of teleosts and contains numerous rods and cones organized in a typical square mosaic (Podugol'nikova & Maximov, 1973). Altogether, 60, 112, and 149 absorption spectra of the outer segments of rods, single cones, and double cones, respectively, were measured. The most representative data satisfying the accepted criteria (Bowmaker et al., 1994; White et al., 2004) were used for estimating the spectral characteristics of visual pigments.

Our estimates showed that all types of photoreceptors comprised spectrally uniform groups with their pigment absorption maxima at 530 ± 5 nm (rods, $n = 14$), 530 ± 6 nm (single cones, $n = 54$), and 570 ± 7/625 ± 5 nm (both double-cone members, $n = 19/10$).

In publications on visual pigments and, in particular, on microspectrophotometric studies, a pigment is usually assigned to a certain group depending on the position of its absorption λ_{max}: ultraviolet- (UV), short-wave- (SWS, blue), middlewave- (MWS, green) and long-wave-sensitive (LWS, red). The accepted terminology is especially useful for indicating pigments contained in different members of the double cones. The categorization of these "spectral groups" of pigments is based on the molecular genetic characteristics of their opsins (Yokoyama, 2000). Because we have no molecular data on the opsins in the masked greenling, we conventionally use the "relative" terminology referring to the most red-sensitive member of the double cones as LWS and another paired member ("less red-sensitive") as MWS.

The MSP data were approximated by templates for vitamin A_1-based visual pigments, except for the values for the LWS member of double cones with a maximum of 625 nm, for which the template for vitamin A_2-based pigments was used. This admission was based on the following.

Firstly, we agreed with the widely accepted opinion that all visual pigments of "fully marine" fishes are based exclusively on

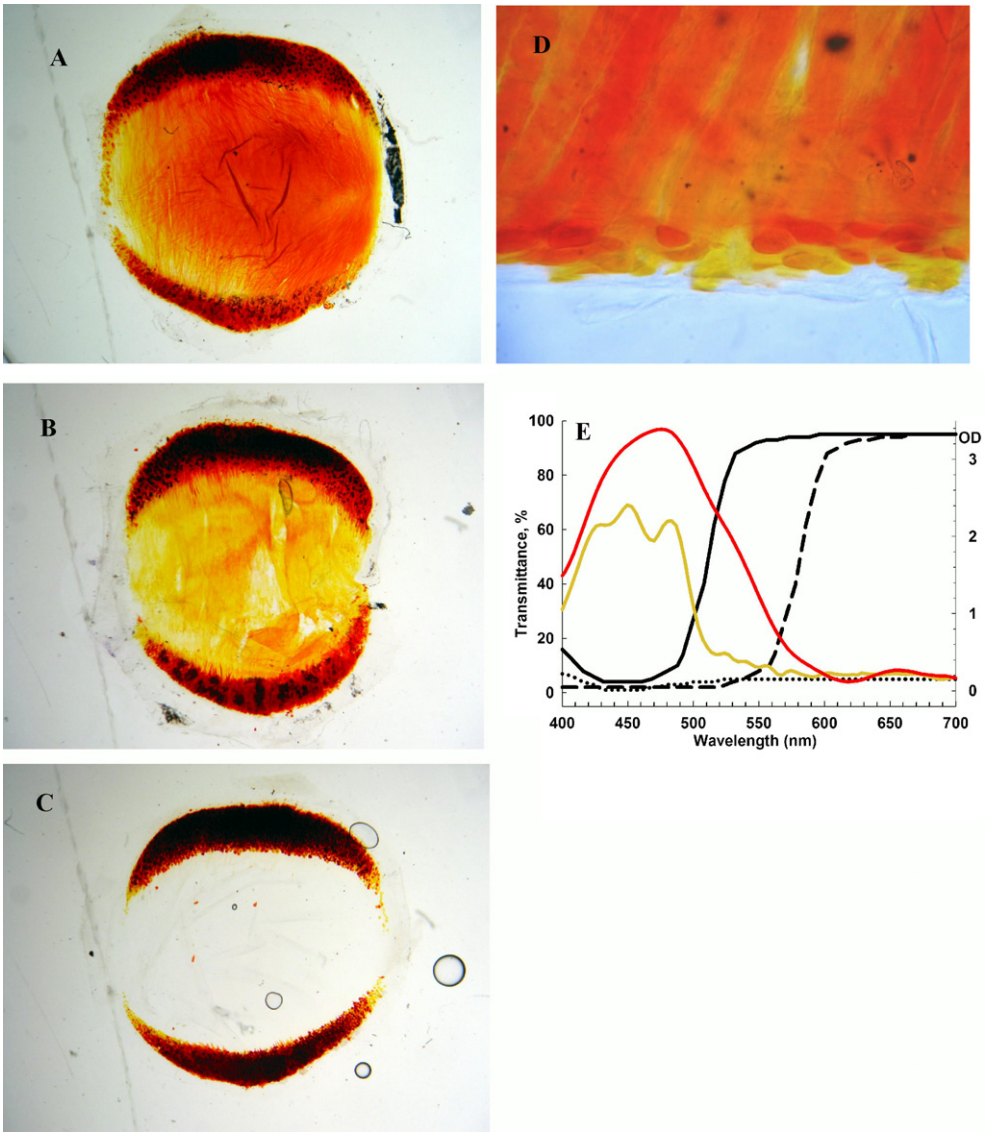

Fig. 1. The colour of the cornea of *Hexagrammos octogrammus* in the light adapted (A) and dark adapted (C) conditions and at twilight (B). (D) Transverse section through the scleral cornea shows separate layers of processes of orange and yellow chromatophores. (E) Transmission (black lines, left ordinate) and optical density (colour lines, right ordinate) of the central cornea of the eye during different stages of light adaptation: solid and yellow lines, twilight; dashed and red lines, full light adaptation, 2 h at direct solar illumination; dotted line, after 2 h at full darkness.

vitamin A_1 (Bowmaker, 1995). Furthermore, bleaching of digitonin extracts of visual pigments of the masked greenling in the presence of hydroxylamine revealed the presence of rhodopsin (Shukolyukov & Tyurin, 1975). Secondly, there is an opinion based on biophysical arguments that the theoretical limit for the λ_{max} of pigments based on vitamin A_1 cannot exceed 582 nm (Blatz & Liebman, 1973; after Loew & Lythgoe, 1978). Therefore, it was reasonable to use porphyropsin templates for all visual pigments with the maxima exceeding this value.

The following approximation of the spectra was performed using a data-processing program (Govardovskii et al., 2000) in which mixed A_1/A_2 spectra could be generated, whereby the λ_{max} difference within an A_1/A_2 pair was determined from its known relations (Harosi, 1994). Because of the considerable "red-sensitivity" of the LWS members of double cones, we had no doubt that they contained porphyropsin. Indeed they appeared to contain a mixture of rhodopsin with a maximum at 560 nm and porphyropsin with a maximum at 625 nm, with a considerable predominance of the latter (85%, Fig. 2D). A similar rhodopsin/porphyropsin ratio, was found in the MWS members of double cones, in the single cones and in the rods (Fig. 2A and B). The paired members of all double cones were the same: they always contained MWS pigment paired with LWS pigment. In some individuals, photoreceptors of all types contained almost pure porphyropsin.

Bleaching experiments in the presence of hydroxylamine also confirmed the presence of porphyropsin in the retina of the masked greenling. We could not get reliable results with single and double cones, obviously because its visual pigments are destroyed when exposed to hydroxylamine (Knowles & Dartnall, 1977).

But the microspectrophotometry of the rods showed the predominance of porphyropsin, judging from the matching of experimental data and the absorbance curve of A_2-oxime (Fig. 2C).

4. Discussion

We have shown that increased long-wave sensitivity is achieved through the porphyropsin predominance in fish caught

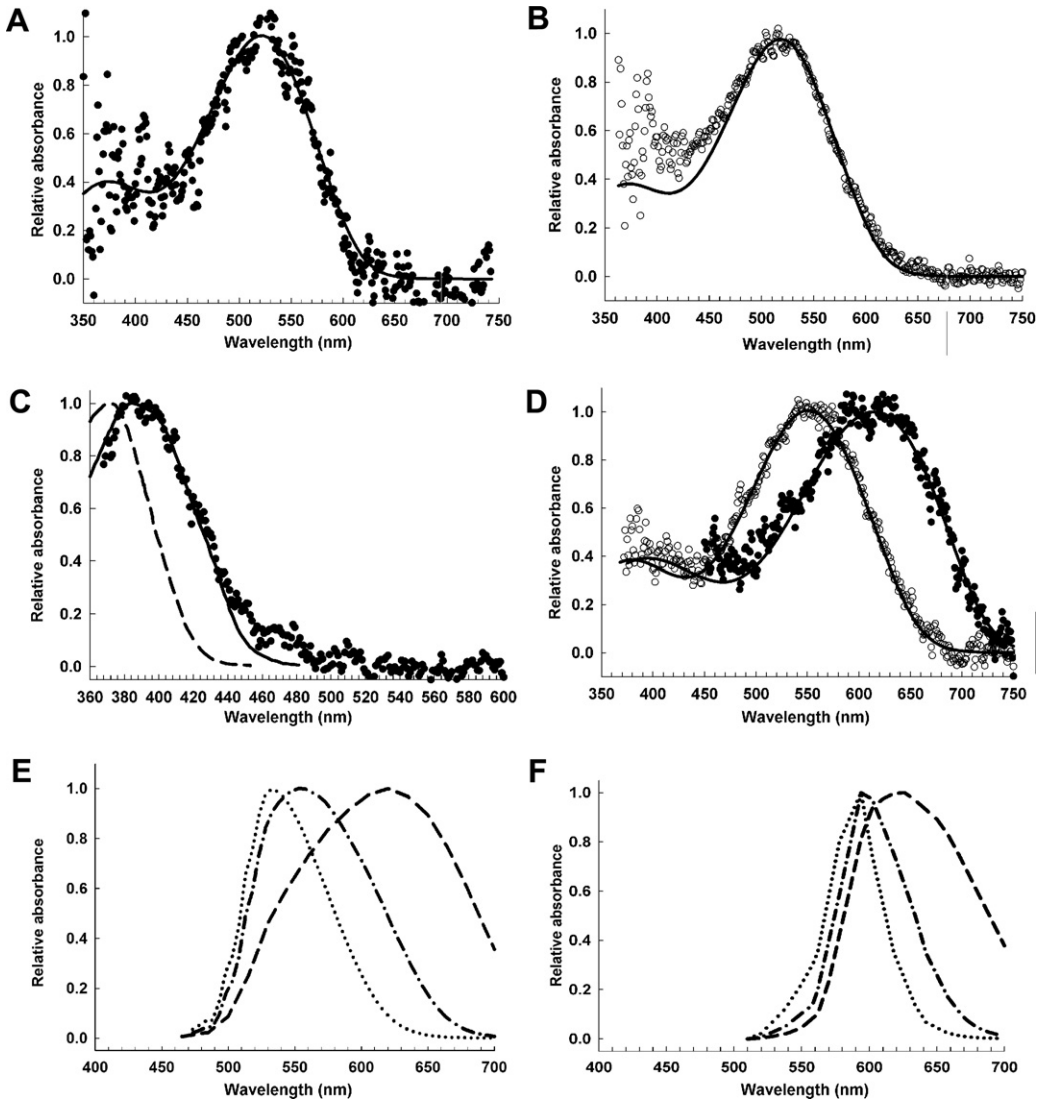

Fig. 2. Microspectrophotometrical data for absorbance spectra of the outer segments of retinal photoreceptors in *Hexagrammos octogrammus*. The spectra are the means of records obtained from separate cone outer segments or from the group of the overlapped rod outer segments. Full curves through the normalized data points at plates A, B and D are best fitting $A_1 + A_2$ pigments template curves. The number of records (n), absorbance (OD) and A_1/A_2 ratio with λ_{max} are shown in brackets. (A) Rods ($n = 20$; $0.1?A_1500 + 0.9?A_2525$). (B) Single cones ($n = 45$; OD = 0.019; $0.18?A_1500 + 0.82?A_2525$). (C) Bleaching of rod outer segments in the presence of 20 mM hydroxylamine. The mean normalized data of 28 records (filled symbols) after full bleaching are combined with normalized absorbance spectra of A_1- and A_2-oximes for reference. Both curves represent original data for oximes in the rod outer segments of the common frog, *Rana temporaria* (A_1-oxime, broken line) and the clawed frog, *Xenopus laevis* (A_2-oxime, solid line) kindly provided by Dr. V.I. Govardovskii. (D) Double cones. Filled symbols, LWS member ($n = 22$; OD = 0.023; $0.15?A_1560 + 0.85?A_2625$); open symbols, MWS member ($n = 38$; OD = 0.034; $0.2?A_1522 + 0.8?A_2562$). (E and F) Calculated effective spectra of cone pigments (normalized). Dashed line, LWS member of double cones; chain line, MWS member of double cones; dotted line, single cones. (E) Twilight (see Fig. 1B and E). (F) Bright light (see Fig. 1A and E).

in May–October, when they are active in shallow waters. Newmetamorphosed youngsters caught at the end of April and adults caught in October had virtually the same pigment ratio. In fish with a mixture of A_1- and A_2-based pigments, their ratio depends on changes in light conditions and water temperature both in the nature and in experiment. This was documented for several freshwater and euryhaline fishes (Allen & McFarland, 1973; Bridges, 1972; Saszik & Bilotta, 1999; Ueno et al., 2005; Whitmore & Bowmaker, 1989), but it is still unclear whether this is also the case in the masked greenling. If the rhodopin/porphyropsin ratio in this species is indeed season-dependent, it must differ from what is known about other fish displaying seasonal variation in pigment ratio, in which rhodopsin predominates in summer and porphyropsin in winter. This question requires a special investigation under controlled conditions.

A comparison of the presented data with characteristics of visual pigments of other shallow-water marine fishes showed the following. According to our preliminary results (Kondrashev, 2005), the mean values of λ_{max} of retinal photoreceptors in over 40 coastal teleost species of the Sea of Japan, bottom-dwelling with the masked greenling at the same depth (0–20) m, made 505 ± 7, 455 ± 16, and 525 ± 13/545 ± 20 nm (mean ± *SEM*) for rods, single cones and doubles cones, respectively. The mean λ_{max} for 38 coral reef fish species were, respectively, 490, 450 (excluding UV-sensitive single cones), and 500–520 nm (Losey et al., 2003). Most shallow-water (littoral) sculpins from the Lake Baikal, closely related to the marine cottid fishes, have corresponding rhodopsins with absorbance maxima at about 450 and 520 nm (Bowmaker et al., 1994). It is evident that spectral sensitivity of the photoreceptors in the masked greenling is considerably (by 20–80 nm for the absorption λ_{max}) shifted to the long-wave region as compared to visual pigments in other marine species studied to date. The LWS member of double cones has the highest red-sensitivity as compared to cones of all known marine fish species studied so far.

What can account for an increase in red-sensitivity in a "fully marine" fish? Most probably, it is due to the presence of extremely dense corneal filters in the masked greenling. Considering the relationship between characteristics of the corneal light filter and the complement of visual pigments, and based on the preliminary results obtained from ERG-recordings from the whole retina in the masked greenling, it was proposed that the region of wavelength discrimination for this fish is markedly shifted to the long-wave region, while long-wave visual pigments of this fish species should have sensitivity peaks at 560 nm and more (Orlov, 1978). The present results strongly confirm this proposal.

Starting from the first descriptions of stained ocular media, namely corneas, numerous opinions were issued on their biological role. Among them, reduction of light dispersion in the short-wave region of the spectrum, enhancement of the visual contrast, and protection from bright illumination (Douglas & Marshall, 1999; Losey et al., 2003; Walls & Judd, 1933). Some biological peculiarities of the masked greenling indicate that its intensively coloured corneal filters may be involved in one or more of these functions. Active predation in the near bottom water requires enhanced vision acuity in this medium of increased turbidity (Gomelyuk, 2000). During daytime, the masked greenling fry stay in the rocky intertidal zone and are thus exposed to very bright illumination (our observations; Gomelyuk & Leunov, 1999). The same impact also affects the adults at shallow spawning grounds (Gorbunova, 1970; Markevich, 2004).

We are not inclined to propose functional roles for the intensely orange screen formed by corneal filter (Fig. 1) other than those proposed for other fishes. It is however, noteworthy that if visual pigments of the masked greenling were "usual", as in the majority of marine fishes, the corneal pigmentation would have significantly degraded cone-driven visual sensitivity and reduced capability for wavelength discrimination in the daylight. The effective spectral sensitivity of cones in the presence of a corneal filter was calculated as the product of the curves on Figs. 1E and 2B, D. These data show that at least two classes of photoreceptors in the greenling would permit wavelength discrimination in twilight (Fig. 2E) and probably even at bright light (with a fully light-adapted cornea) (Fig. 2F). The latter state of the cornea is typical of the masked greenling because it is a strictly diurnal fish dwelling from spring to autumn at a depth of 0–10 m (Gomelyuk et al., 1989; Markevich, 2004). Obviously, if the cones of the masked greenling contained only A_1-pigments, then its λ_{max} would change to 500, 522, and 560 nm resulting in further worsening of visual abilities.

The coastal waters of the Sea of Japan where the masked greenling occurs are assigned to the water Type J1 in spring and summer and to Type J3 in winter (Jerlov, 1976; Titlyanov, Novozhilov, & Cherbadgy, 1993). These waters receive sufficient long-wave illumination at shallow depths. The estimations of the downwelling spectral irradiance at various depths show that in summer down to 10 m deep, long-wave illumination in the region overlapped by sensitivity of cones exceeds the photopic threshold by 2 log units or more (Dartnall, 1975) even allowing for the "cut-off"-effect of the corneal filter (520–700 nm).

Since rods and cones share the same pool of chromophore in the retinal pigment epithelium (Loew & Dartnall, 1976; Provencio, Loew, & Foster, 1992), the rod absorption spectrum in the greenling is also red-shifted and potentially reduced during the day due to an increased optical density of the cornea. However, at low light levels when rods actually function, these effects on spectral absorption would be neutral because the changeable cornea does not maintain its extreme optical density under these conditions (Orlov & Gamburtzeva, 1976; see also Fig. 1C).

The presence of a rhodopsin–porphyropsin system in the retina and, as a sequence, a shift of sensitivity of the photoreceptors to the long-wave region of the spectrum, is common for many freshwater, euryhaline, and anadromous fish species (Bowmaker, Dartnall, & Herring, 1988; Wald, 1939). However, it is not typical of "fully" marine teleosts. Besides the case of the masked greenling described here, the phenomenon was reported only for the peacock blenny (White et al., 2004), surfperches (Cummings & Partridge, 2001), several species of wrasses (Labridae), parrot fishes (Scaridae), trigger fish (Balistidae) (Muntz & McFarland, 1977), and mesopelagic stomiid dragon fishes of the genera Aristostomias, Malacosteus, and Pachystomias (Bowmaker et al., 1988; Partridge & Douglas, 1995). In the latter, in contrast to other pigment-pair systems, different pigments are present in different cell classes (rods). In some fishes, possessing rhodopsin–porphyropsin mixtures, the adaptive significance of the presence of porphyropsin and the enhancement of red-sensitivity could be determined by the presence of the optical filtering. This could be true for both the greenling and wrasses, in which corneal colouration of reasonable density was also described (Gnyubkina & Gamburtzeva, 1981; Kondrashev et al., 1986; Moreland & Lythgoe, 1968; Muntz, 1976; Siebeck & Marshall, 2000, 2001) but in most cases this significance is not always clear (Loew, 1995). The masked greenling and stomiid fishes demonstrate the highest degree of useful specialization of the visual pigment system directed to the maximal use of the quantum flux in the long-wave region of the spectrum and, consequently, an enhancement of visual abilities. Further comparative studies are needed to shed more light on the relationship between properties of the ocular media (in the present case, cornea), nature of visual pigments, and ecology. The present study is the first to deal with the visual pigment system in one greenling species broadly distributed in nearshore benthic communities of subarctic and temperate waters of the North Pacific Ocean. It is not excluded that similar "red-shifted" visual pigment systems may be found also in closely related species as well in some representatives of other taxa (family Stichaeidae; order Tetraodontiformes) that have intensely coloured corneas of changeable optic density (Appleby & Muntz, 1979; Kondrashev et al., 1986; Siebeck et al., 2003).

Acknowledgments

The author wishes to thank V.O. Pois (IMB FEB RAS), Dr. V.I. Govardovskii (Institute of Evolutionary Physiology and Biochemistry, RAS), and A.K. Panyutin (Institute of Information Transmission Problems, RAS) for providing the original computer programs and for setting the electronic equipment. My thanks are also due to Dr. N.S. Shelud'ko for the opportunity to use the research facilities of the Laboratory of Cell Biophysics at the Marine Biological Station "Vostok", to Dr. A.S. Sokolovsky and E.G. Reizman (all from IMB FEB RAS) for their help in catching fish. Special thanks are to I.A. Barsegova and Dr. Michael Huggins who provided valuable improvements to our English. The study was supported by the grants of the Russian Foundation for Basic Research (No. 07-04-00068) and Far East Branch of RAS (No. 06-I-OBN-093) in the framework of the program of the Department of Biological Sciences of RAS.

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